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## Review

## Evolution of color and vision of butterflies

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**Abstract**

Butterfly eyes consist of three types of ommatidia, which are more or less randomly arranged in a spatially regular lattice. The corneal nipple array and the tapetum, optical structures that many but not all butterflies share with moths, suggest that moths are ancestral to butterflies, in agreement with molecular phylogeny. A basic set of ultraviolet-, blue- and green-sensitive receptors, encountered among nymphalid butterflies, forms the basis for trichromatic vision. Screening pigments surrounding the light-receiving rhabdoms can modify the spectral sensitivity of the photoreceptors so that the sensitivity peak is in the violet, yellow, red, or even deep-red, specifically in swallowtails (Papilionidae) and whites (Pieridae), thus enhancing color discriminability. The photoreceptor sensitivity spectra are presumably tuned to the wing colors of conspecific butterflies.

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*Keywords:* Visual pigments; Corneal nipples; Tapetum; Wing color; Spectral sensitivity

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**1. Introduction**

Butterflies include the most colorful living objects and never fail to charm the spectator, especially because of their association with flowers. It thus has been a long-standing assumption that butterflies possess color vision, but that this is indeed the case has only recently been demonstrated unequivocally (Kelber and Pfaff, 1999; Kinoshita et al., 1999). Unfortunately, the neural systems mediating color vision have remained virtually unexplored, but our knowledge about the photoreceptor systems and their possible evolution is steadily accumulating (Briscoe and Chittka, 2001). The differences in the eyes of butterflies studied so far suggest that the capacity to discriminate colors varies among species, which is understandable, as different behaviors and habitats impose different visual tasks (Arikawa, 2003).

The diversity in butterfly species is extremely rich, and studies of the anatomy, physiology and development of butterfly eyes and optical ganglia (Yagi and Koyama, 1963; Strausfeld and Blest, 1970; Arikawa, 1999; Briscoe and Chittka, 2001; Warrant et al., 2003) as well as of the architecture and development of the wings and their scale cells indicate the great potential of butterflies for understanding central questions of evolution and development (Nijhout, 1991; Brakefield et al., 1996).

Butterflies belong to the insect order Lepidoptera, but most of the lepidopteran families are moths. There is considerable evidence that the moths are ancestral to the butterflies. The evolutionary tree of moths branches off into the rhopalocerans, i.e., the Hedyliidae, Hesperidae (the skippers), and Papilionoidea; the latter superfamily consists of the butterfly families Papilionidae, Pieridae, Nymphalidae, Lycaenidae, and Riodinidae (Wahlberg et al., 2005).

Most butterflies are adorned with bright wing colors, which are presumably tuned to the properties of the visual systems of observers, be they potential partners or predators. Notably, intraspecies recognition is often achieved via the displayed wing

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colors, and this will be especially the case in butterfly species with sexual dichroism, that is, where the sexes have markedly different colors (Obara and Majerus, 2000; Kemp et al., 2005).

In this paper we will first describe the anatomy of butterfly eyes and the properties of the photoreceptors and their visual pigments. Subsequently, we will present a comparative survey of the eyes of butterflies and related insect species, with a perspective on the spectral properties of butterfly wings.

## 2. The butterfly eye and retina

### 2.1. Anatomy of butterfly eyes

The compound eyes of butterflies consist of numerous anatomically identical units, the ommatidia, which are more or less arranged in a hemisphere. Each ommatidium is recognizable from the outside by a facet lens. Together with the associated crystalline cone the facet lens forms the imaging optics that projects incident light onto the photoreceptors (Fig. 1).

A butterfly ommatidium contains nine photoreceptors. Their light-sensitive organelles, the rhabdomeres, jointly constitute the fused rhabdom, a long cylinder that acts as an optical waveguide. Depending on the quality of the imaging optics as well as the size of the rhabdom, each ommatidium samples a different spatial area, with widths typically of the order of  $1^\circ$ . The visual fields remain restricted owing to pigment cells that surround each ommatidium as a protective light screen (Land, 1981; Nilsson, 1989).

A specialty of most butterfly eyes is the presence of a tapetum located proximally to the rhabdoms. Incident light propagates along the rhabdom, and when it is not absorbed it is reflected by the tapetum. The light travels then in the reverse direction and, if not absorbed, eventually leaves the eye again, where it is visible as eye shine (also called eye glow).

### 2.2. Spectral receptor classes and eye regionalization

Vision starts with the absorption of light by the visual pigments, which are localized in the rhabdomere, a special, strongly folded part of the photoreceptor cell membrane. The visual pigments, rhodopsins, are opsin proteins combined with a chromophore. In humans and bees this is retinal and in lepidopterans it is 3-hydroxyretinal, derivatives of vitamins A1 and A3, respectively (Vogt, 1989; Seki and Vogt, 1998). Photon absorption by the rhodopsin causes isomerization of the chromophore and subsequently a photochemical process that ends in a photostable metarhodopsin. The metarhodopsin (M) can be photoreconverted to the rhodopsin (R) state (Fig. 2).

The general organization of butterfly color vision is similar to that of honeybees and bumblebees. The bee color vision system is based on three photoreceptor classes, with maximal sensitivity in the ultraviolet (UV), blue (B) and green (G) wavelength ranges (Menzel and Backhaus, 1989; Spaethe and Briscoe, 2005). Extensive electrophysiological recordings in a large number of hymenopteran species have demonstrated the universal presence of the three basic receptor classes

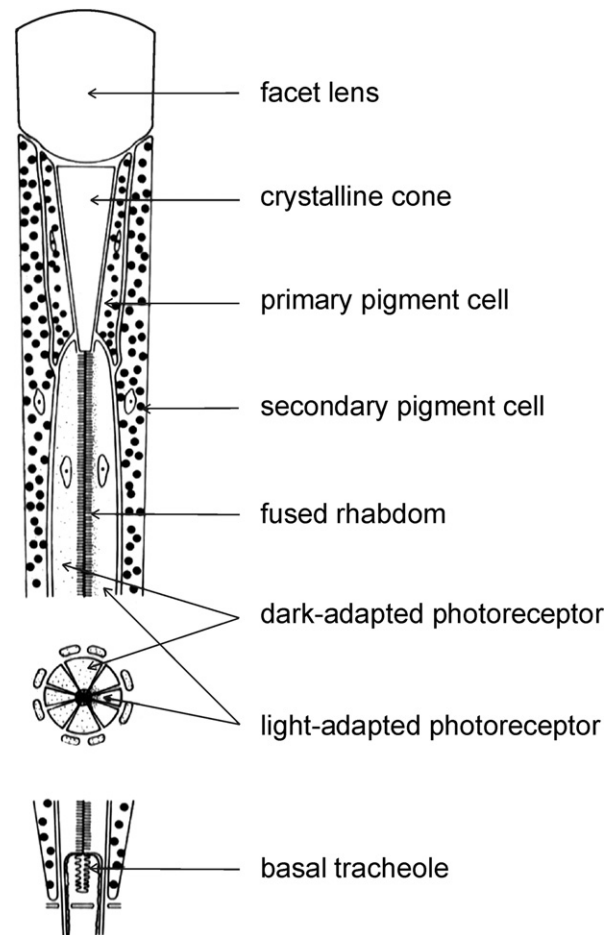


Fig. 1. Anatomy of an ommatidium of a diurnal butterfly. The facet lens focuses incident light into the rhabdom. This is the cylindrical structure that consists of the rhabdomeres of the photoreceptors, which are fused together. The rhabdomere is the organelle that contains a photoreceptor's visual pigment. The fused rhabdom acts as an optical waveguide, which functions to enhance the chance of light absorption by the visual pigments, and thus to enhance light sensitivity. Proximally of the rhabdom a basal tracheole exists, which acts as a reflector for light that has not yet been absorbed. Part of the reflected light is not absorbed at the way back, and this light leaves the eye again, so that it is visible as eye shine.

(Peitsch et al., 1992). Intracellular electrophysiology of photoreceptors of nymphalid butterflies has demonstrated a similar basic set of UV, blue and green receptors (Kinoshita et al., 1997).

The distribution of receptor types appears not to be homogeneous, however. For instance, in the eyes of the honeybee drone, which are divided into a dorsal and ventral eye half, the set of UV-, B- and G-receptors is only present in the ventral eye, whilst the dorsal half only has UV- and B-receptors (Peitsch et al., 1992), in line with optical observations (Menzel et al., 1991). Similar regionalizations, often sex-related, have been encountered in many insect species (Stavenga, 1992). Specialized dorsal areas can be readily observed in butterfly eyes by utilizing the eye shine, for instance in the small white *Pieris rapae* and the satyrine *Bicyclus anynana* (Miller, 1979; Stavenga, 2002a,b).

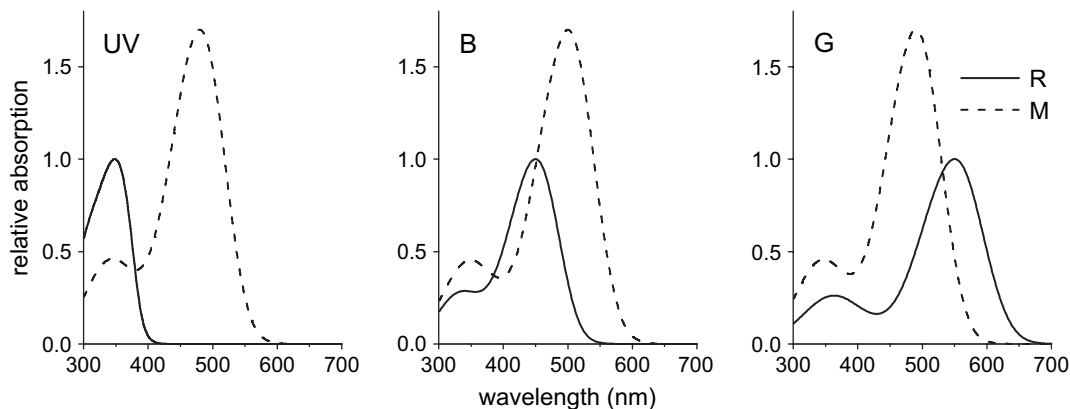


Fig. 2. The basic set of three visual pigments employed by many insect eyes, namely an ultraviolet- (UV), blue- (B), and green- (G) absorbing rhodopsin, absorbing maximally at roughly 350, 450 and 550 nm, respectively. The metarhodopsins (M), thermostable forms of the rhodopsins (R), are assumed to absorb maximally at 480, 500, and 490 nm, respectively. Spectrophotometry of insect visual pigments has invariably shown that the peak absorption of the metarhodopsins relative to the peak absorption of their rhodopsin is distinctly larger than 1. The shapes of both the rhodopsin and the metarhodopsin spectra were derived with the template formula of Govardovskii et al. (2000).

A very special area is the dorsal rim, consisting of a few rows of ommatidia, where the photoreceptors have a very high polarization sensitivity. Dorsal rims were first discovered in hymenopterans, but were later shown to be widespread among insects, including lepidopterans (Kolb, 1986; Hämmerle and Kolb, 1988). The photoreceptors in the dorsal rim mediate polarization vision (Labhart and Meyer, 1999), and in lepidopterans their spectral sensitivity appears to be restricted to the ultraviolet (Stalleicken et al., 2006), as is the case in flies (Hardie, 1985) and bees (Rossel, 1989).

### 2.3. Visual and filter pigments

The general rule is that each photoreceptor cell uses no more than one visual pigment, although there are a few notable exceptions where multiple visual pigments are expressed in one and the same photoreceptor (Kitamoto et al., 1998; Arikawa et al., 2003; Sison-Mangus et al., 2006). In situ hybridization studies with selective RNA probes can identify the distribution and localization of the spectral receptor classes in the compound eye ommatidia. A most curious property of insect ommatidia has thus emerged, namely that the visual pigment expression patterns are not identical in different ommatidia, even though the anatomy of the ommatidia seems virtually indistinguishable. In general, three types of ommatidia are identified, locally arranged in a random, heterogeneous lattice (butterflies: Arikawa and Stavenga, 1997; Arikawa, 1999; Kitamoto et al., 2000; Qiu and Arikawa, 2003b; Briscoe and Bernard, 2005; Sauman et al., 2005; moths: White et al., 2003; bees: Spaethe and Briscoe, 2004; Wakakuwa et al., 2005). The emerging picture for nymphalid butterflies, moths and bees is that while basically six of the nine photoreceptors in all three ommatidial types express a green-sensitive (long-wavelength absorbing) visual pigment, the heterogeneity is created by differences in the short-wavelength receptors: one ommatidial type contains one UV and one blue receptor, the second type has two blue receptors

and the third ommatidial type harbors two UV receptors. A plausible functional interpretation of this diversity has not yet been elaborated. The property of the ninth receptor is not clear at the moment.

The relative location of the rhabdomeres within the rhabdom is a family characteristic. In bees, eight photoreceptors contribute their rhabdomeres over most of the length of the rhabdom, whilst the rhabdomere of the ninth photoreceptor only exists near the basement membrane, which limits the retina at the proximal side. Many nymphalid butterflies have the same organization with parallel rhabdomeres, but in monarchs the short-wavelength receptors have rhabdomeres that are somewhat restricted to the distal part of the rhabdom, whereas the rhabdomeres of the longer wavelength receptors are more dominant in the proximal part of the rhabdom (Sauman et al., 2005).

An extreme segregation with four distal and four proximal rhabdomeres exists in the so-called tiered rhabdoms of pierid and papilionid butterflies. The functional reason of the relative positioning of the rhabdomeres must be sought in the fact that the rhabdomeres are part of one optical waveguide and that they have different visual pigments. Because pigments absorb light, the distal rhabdomeres act as optical filters for the proximal rhabdomeres. This can sharpen the spectral sensitivity curves of the individual photoreceptors, and thus will improve spectral discrimination. The rhabdom organization of bees and nymphalid butterflies is presumably ancestral to that of the more complicated rhabdoms of the pierids and papilionids, which have tiered rhabdoms and diverse optical filter systems, the themes of the following sections.

### 2.4. Ommatidial heterogeneity

The small white, *P. rapae crucivora*, a subspecies living in Japan, is a prominent example of a species with a heterogeneous retina. Three types of ommatidia are encountered in the fronto-ventral retina, with trapezoid, square and

rectangularly-shaped rhabdoms (Table 1). The difference in rhabdom shape is related to the different characteristics of the R1 and R2 photoreceptors. In type I ommatidia R1 and R2 form a pair of UV and blue receptors, in type II ommatidia both R1 and R2 are either violet receptors (in females) or double-peaked blue receptors (in males), whilst in type III ommatidia both are ultraviolet receptors (Arikawa et al., 2005; Qiu and Arikawa, 2003b). The difference between female and male type II R1 and R2 receptors is due to a violet absorbing, blue–white fluorescing pigment, which is male-specific (Table 1, Fig. 3). The pigment functions as a spectral filter for the violet rhodopsin present in the R1 and R2 of type II ommatidia (Arikawa et al., 2005). The short-wavelength receptors presumably function, among others, in sexual recognition, because the color of the wings of *P. rapae* characteristically changes in the violet wavelength range (see Section 4).

As judged from the homogeneous eye shine (Stavenga, 2002a,b; Sauman et al., 2005), nymphalids have simpler eyes than many other butterfly species, where different types of screening pigment within the photoreceptors create a multi-colored eye shine, thus demonstrating the heterogeneity of the retina (Stavenga, 2002a). Nevertheless, in situ hybridization studies of visual pigments show that nymphalids, as for example the painted lady, *Vanessa cardui* (Briscoe et al., 2003), and the monarch, *Danaus plexippus* (Sauman et al., 2005), exhibit a diverse organization of the short-wavelength photoreceptors. The retina of the hawkmoth *Manduca sexta* has a very similar heterogeneity (White et al., 2003).

The retinal heterogeneity is most elaborate in the Japanese yellow swallowtail, *Papilio xuthus*. Its short-wavelength photoreceptors are distributed in three ommatidial classes, where three types of photoreceptor screening pigments populate the diverse ommatidia: a yellow-colored, a red-colored, and a colorless pigment; the latter absorbs in the ultraviolet and is weakly fluorescing. Furthermore, the proximal long-wavelength receptors use different rhodopsins and, on top of that, a number of photoreceptors even express multiple visual pigment types (for details see Arikawa, 2003; Arikawa et al., 2003).

### 2.5. Spectral modifications by optical filtering

The spectral sensitivities of the receptors are frequently modified by the action of spectral filters, which is sometimes combined with the expression of multiple visual pigments. An exemplary case is the small white, *P. rapae*. The rhabdoms in the main, fronto-ventral part of its eye are surrounded by red pigment granules, which function as red transmitting filters (Ribi, 1979). The rhabdoms in *P. rapae* are tiered (Fig. 3a), such that the rhabdomeres of four receptors, numbered R1–4, make up the distal tier, and the rhabdomeres of four other receptors, called R5–8, constitute the proximal tier (Table 1); the ninth photoreceptor, R9, contributes a very minor basal part of the rhabdom (Qiu et al., 2002).

The R3–8 photoreceptors of all ommatidia express a green rhodopsin, with a peak absorption at 563 nm. The red screening pigment that surrounds the rhabdom in predominantly the distal part of the ommatidium effectively suppresses the light sensitivity at the short wavelengths, resulting in a strong red shift of the spectral sensitivity of the R5–8 receptors (Fig. 3b). Actually, *P. rapae* has two types of red pigment filters, pale-red (PR) and deep-red (DR), causing two classes of R5–8 red receptors, with narrow-band sensitivity spectra peaking at about 620 and 640 nm, respectively (Wakakuwa et al., 2004). Whether an ommatidium contains the pale-red or deep-red pigment filter can be directly recognized in vivo by epi-illumination microscopy (Stavenga et al., 2001). Epi-illumination with white light results in a colored eye shine, which betrays the color of the filter, as only the non-absorbed light is observed. The ommatidia in the main part of the eyes of *P. rapae* reflect either pale-red or deep-red light (Stavenga, 2002b).

Red screening pigment granules, concentrated in clusters in the photoreceptor somata near the rhabdom, and acting as optical filters on the light flux propagating in the rhabdom waveguide (Fig. 3a), are found in a wide variety of insect species. This mechanism has therefore probably evolved independently in several occasions. For instance, one group of ommatidia in the sphecid wasp *Sphex cognatus* has red pigment clusters lining the rhabdom, whilst the complementary

Table 1  
Ommatidial types and photoreceptor properties of the small white, *Pieris rapae crucivora* (after Qiu and Arikawa, 2003b; Wakakuwa et al., 2004)

Ommatidial type	I			II			III		
Rhabdom shape	Trapezoid			Square			Rectangular		
Pigmentation	Pale-red			Deep-red			Pale-red		
Sex	Female/male			Female		Male	Female/male		
Fluorescing pigment	No			No		Yes	No		
Photoreceptor	S	opsin		S	opsin		S	opsin	
R1	UV <sup>a</sup>	PrUV		V	PrV		dB	PrV	
R2	B <sup>a</sup>	PrB		V	PrV		dB	PrV	
R3,4	Y	PrL		Y	PrL		Y	PrL	
R5–8	PR	PrL		DR	PrL		DR	PrL	

The spectral sensitivities, S, of the ultraviolet (UV), violet (V), blue (B), and yellow (Y) sensitive photoreceptors are well approximated with visual pigment spectra peaking at  $\lambda_{\text{max}}$  = 356, 426, 452, and 563 nm, respectively, and therefore the peak wavelengths of the absorption spectra of the visual pigments, PrUV, PrV, PrB and PrL, will have very similar values. Pale-red (PR) and deep-red (DR) receptors result due to filtering by the pale-red and deep-red screening pigment.

<sup>a</sup> The R1 of type I ommatidia alternatively expresses PrB and the spectral sensitivity then peaks in the blue; in that case the accompanying R2 expresses PrUV and the spectral sensitivity then peaks in the UV. The R9 photoreceptors presumably express PrL.



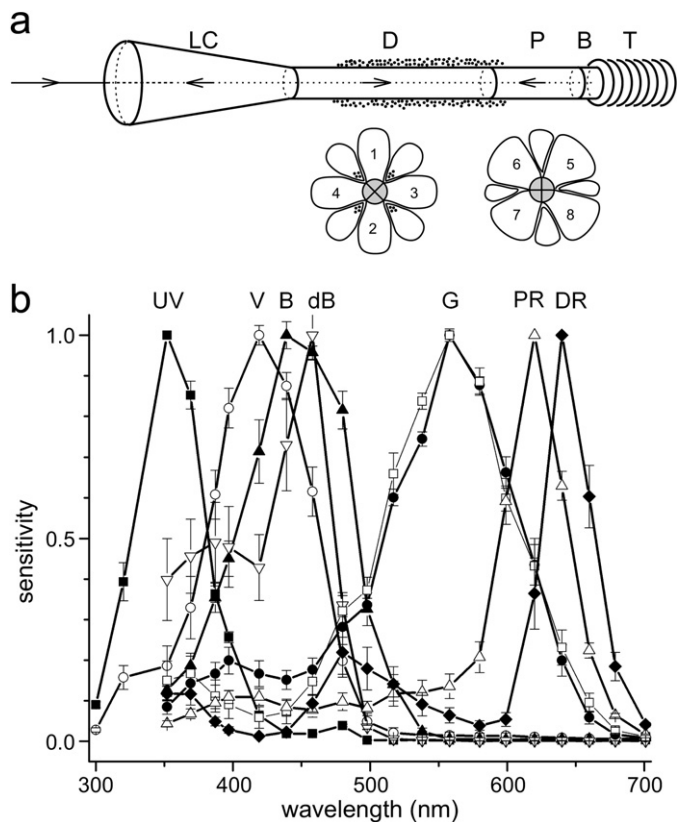


Fig. 3. Light flux in an ommatidium of the small white butterfly, *Pieris rapae*, and photoreceptor spectral sensitivities. (a) Diagram of an ommatidium in longitudinal section (top) and cross-section (bottom). The facet lens and crystal-line cone (LC) channel light into the rhabdom. The distal part of the rhabdom (D) consists of the rhabdomeres of photoreceptors R1–4, the proximal part (P) consists of the rhabdomeres of photoreceptors R5–8, and the basal part (B) fully consists of the rhabdomere of photoreceptor R9. The soma of R5–8 photoreceptors in the distal part of the retina contains clusters of either pale-red or deep-red pigment. The pigments filter light propagating along the rhabdom, as can be seen from incident light reflected by the tapetum (T) that leaves the eye as eye shine (arrows). (b) Spectral sensitivities of photoreceptors in the main, fronto-ventral eye of male and female *Pieris rapae crucivora* determined by intracellular recordings. The dorsal R1 and R2 photoreceptors of the female are either ultraviolet (UV), violet (V) or blue (B) sensitive, the R3–4 are green (G) sensitive, and the R5–8 are either pale-red (PR) or deep-red (DR) sensitive (see Table 1). The male has the same set of photoreceptors, except for the violet receptor, which is modified into a double-peaked blue (dB) receptor (Qiu et al., 2002; Qiu and Arikawa, 2003a; Wakakuwa et al., 2004).

group of ommatidia lacks the pigmentation (Ribi, 1978a); *S. cognatus* has a class of red sensitive receptors most probably resulting from the red filters acting on photoreceptors with a green-absorbing rhodopsin (Ribi, 1978b). A comparable, though somewhat different arrangement has been found in *P. xuthus*, where the clusters of pigment granules that huddle near the rhabdoms are either yellow or red (Arikawa and Stavenga, 1997). The blue- and green-absorbing red pigment is responsible for the red sensitive photoreceptors. Another butterfly species where red pigment filters were demonstrated by anatomy is the monarch, *D. plexippus* (Sauman et al., 2005). Red filters appear ubiquitous among butterflies as follows from microspectrophotometry of the eye shine (Stavenga et al., 2001; Stavenga, 2002a,b).

### 3. Evolutionary considerations

#### 3.1. Visual pigments

Molecular phylogeny indicates that invertebrate visual pigments can be divided into two main groups: long-wavelength (green, G) absorbing and short-wavelength absorbing visual pigments; the short-wavelength set consists of an ultraviolet (UV)- and blue (B)-absorbing group (Fig. 4). The three clades, UV, B and G, presumably developed from ancestral opsins, and form the basis for the basic, trichromatic vision of bees and hymenopterans (Briscoe and Chittka, 2001). Diversification of the trichromatic system occurred by gene duplication. In Papilionidae the G-pigments diversified into green- and red-absorbing visual pigments (Briscoe, 2001), in Pieridae the blue-absorbing visual pigments divided into blue and violet rhodopsins (Fig. 4, Arikawa et al., 2005), and in Lycaenidae the blue visual pigment duplicated into a blue and blue–green rhodopsin (Sison-Mangus et al., 2006). Further functional diversification of the spectral sensitivity of the photoreceptors was achieved by inserting spectral filters in front of or within the photoreceptive structures.

#### 3.2. Apposition and superposition eyes

Butterflies and moths are lepidopterans, but their eyes distinctly differ. In butterfly eyes, neighboring dioptric systems focus light from adjacent parts of the environment on their respective rhabdoms, and thus the eyes are called apposition eyes. In moths, a rhabdom receives light via numerous facet lenses and crystalline cones, and therefore moth eyes are called superposition eyes (Fig. 5). The number of participating facets depends on the species, and within a species on the state of light/dark adaptation. The light flux in moth eyes is commonly regulated by movable sheets of screening pigments, which block the light traversing the so-called clear zone, located in between the crystalline cones and the rhabdom layer. The rhabdoms in the superposition eyes of moths are much fatter than the rhabdoms of the apposition eyes of butterflies, suggesting a higher chance of light capture. Indeed, the large number of facet lenses contributing to a superposition image forms an aperture that is much wider than that of a single facet lens, and this endows the superposition eyes with an obvious, principal advantage over the apposition eyes. Their enhanced light sensitivity allows vision at low light levels (Land and Nilsson, 2002; Warrant et al., 2003).

The high light sensitivity of the superposition eyes of moths is intimately related to a nocturnal life style, whilst the much lower light sensitivity of the apposition eyes of butterflies is related to a diurnal life style. The division is not strict, however, because there are several moth species with superposition eyes that are only active during the day, for instance the sphingid *Macroglossum stellatarum* (Warrant et al., 1999). Also, the diurnal skipper butterflies are equipped with superposition eyes (Horridge et al., 1972). From the observation that the rhabdoms are rather slim in the

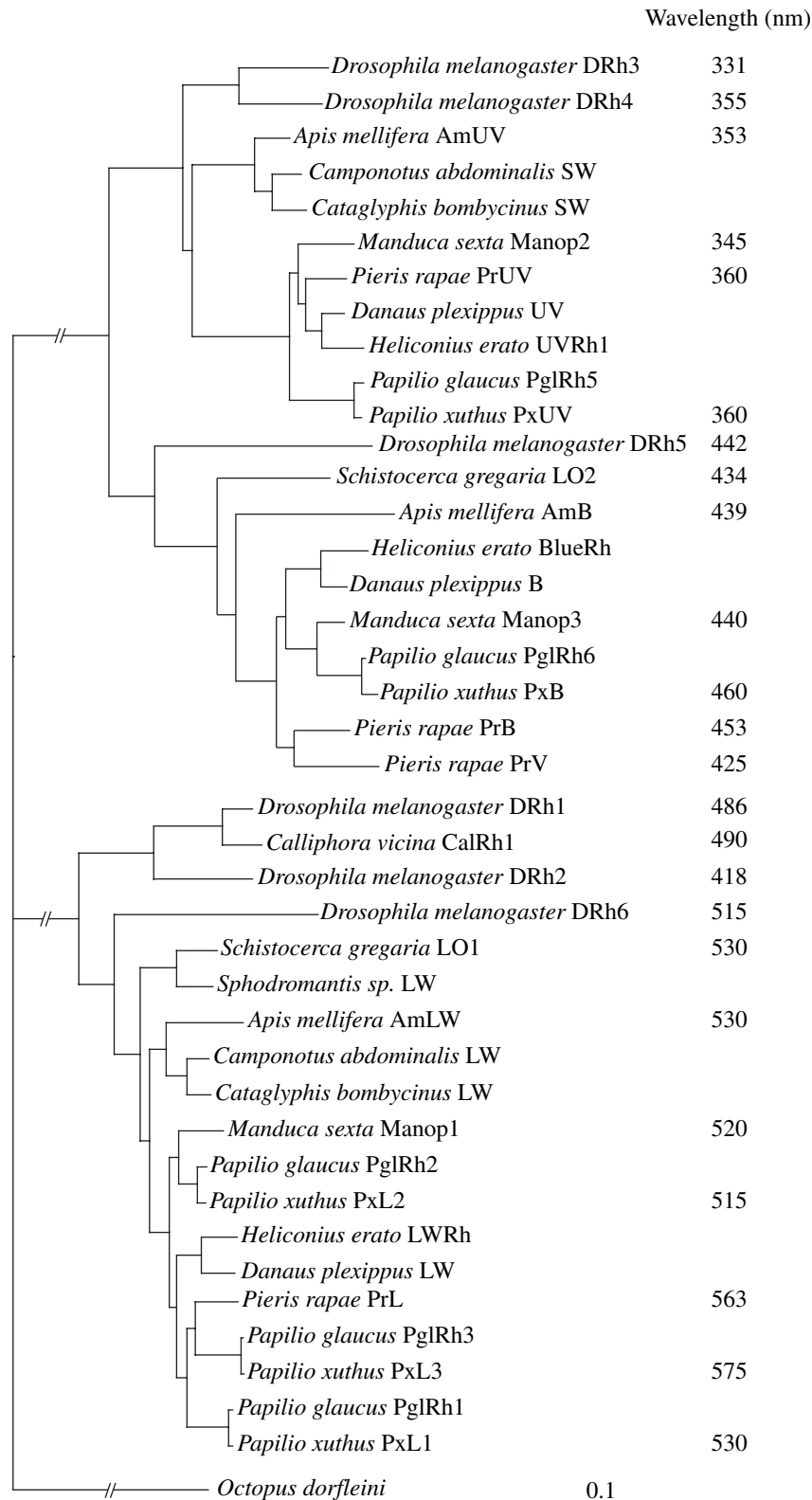


Fig. 4. Phylogenetic relationship of insect visual pigment opsins with absorption peak wavelengths (modified from Arikawa et al., 2005; see also Sison-Mangus et al., 2006).

superposition eyes of diurnal lepidopterans, we can conclude that the high light sensitivity of the superposition eye is not always beneficial and that the photosensitivity has been reduced for the diurnal conditions.

Whether the apposition or the superposition eye type of lepidopterans is ancestral is unresolved. This question can be illustrated by three specific elements of the eyes, namely the corneal nipple array of the facet lenses, the crystalline cone, and the tapetum.

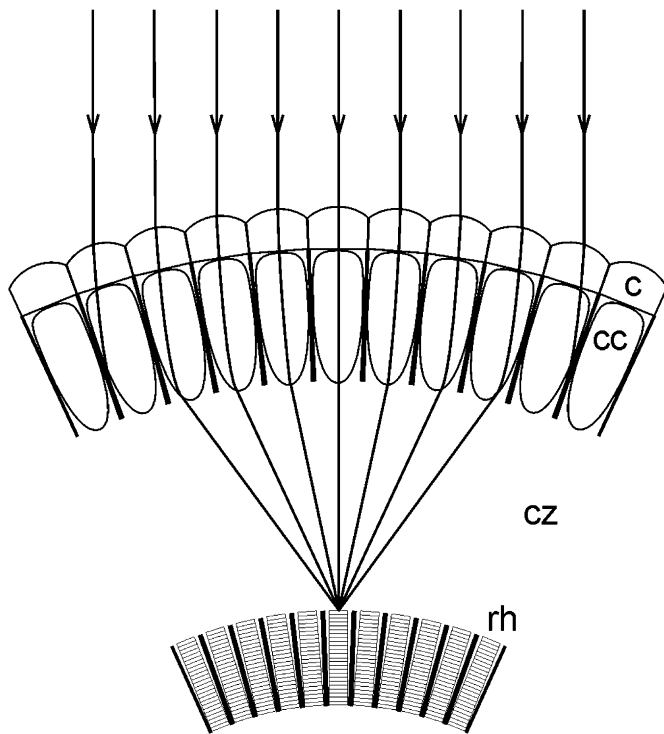


Fig. 5. Diagram of the refracting superposition eye of moths (in the dark-adapted state). Light entering an eye first passes the corneal facet lenses (c) and subsequently the crystalline cones (cc). Proximally of the array of crystalline cones is the clear zone (cz) and the layer of rhabdoms (rh). A beam of light parallel to the optical axis of an ommatidium is focused on the rhabdom of the central ommatidium. Sheets of screening pigment surround the crystalline cones. In many species, tracheolar tapeta and/or screening pigment isolate the rhabdoms from each other.

### 3.3. The corneal nipple array

The facet lenses of virtually all moth species have an outer surface that is densely studded with protuberances of height 250 nm and distance 200 nm (Bernhard et al., 1970). This corneal nipple array forms a smooth optical interface between air and facet lens material, because the nipple dimensions are smaller than the wavelengths of visible light. The array causes a gradually changing refractive index, so that the reflectance of the facet lens surface is effectively reduced. The principal biological function of the corneal nipple array is presumably to reduce the eye glare of the moths in the daytime, so to minimize the visibility for predators (Miller, 1979).

Many butterfly species also feature a corneal nipple array, but the nipple height severely varies between species; the nipples are even absent in the papilionids (Bernhard et al., 1970; Fig. 6). Apparently the corneal nipple array is a trait that is partly (nymphalids, lycaenids) or fully (papilionids) lost during the process of evolution. This may not be surprising for diurnally active and often highly colored animals when the only biological function is the suppression of the corneal reflectance (Stavenga et al., 2005).

### 3.4. The crystalline cone

The crystalline cones of the superposition eyes of moths have a gradient refractive index so that the direction of

incident light is inverted with respect to the cone's optical axis (Kunze, 1979). Nilsson (1989) demonstrated that the crystalline cones of the apposition eyes of butterflies have a similar (though less excessive) gradient refractive index, and he thus suggested that the butterfly apposition eye is ancestral to the superposition eye. On the other hand, Yagi and Koyama (1963), who performed an extensive comparative survey of lepidopteran compound eyes, concluded from anatomical investigations on the post-embryonic development of moth and butterfly eyes that 'the butterfly is a more evolved group than the moth group' (Yagi and Koyama, 1963, p. 231), in line with recent molecular biological analyses (Wahlberg et al., 2005).

An alternative explanation for the refractive index gradient in butterfly cones may be that the gradient is a remnant of the excessive gradient in the moth cones. All the same, it is quite conceivable that an apposition-like organization preceded the development of the superposition eye, where the rhabdoms became separated from the crystalline cones, thus creating a clear zone. The apposition eye type then is the more ancient eye type. Such a hierarchy can in fact be recognized in eyes displaying intermediate cases. For instance, the eyes of both sexes of the mayfly *Baetis vernus* (Ephemeroptera) have so-called lateral eye parts with an apposition eye structure, but the adult male has in addition dorsal eye parts with superposition optics. In the development from subimago to adult the lateral eyes hardly change, but in the dorsal eye the clear zone is enormously expanded, showing that an apposition eye can develop into a superposition eye (Burghause, 1981). Possibly, therefore, the apposition eye type is ancestral to the moth superposition eye, and the apposition eye of the butterflies evolved from the moth superposition eye (see Nilsson, 1989; Land and Nilsson, 2002).

### 3.5. The tapetum

Typical for the eyes of nocturnal animals is the presence of a tapetum, a reflecting layer positioned proximally of the photoreceptor layer. Moth eyes have extensive tapeta, created by air-filled tracheoles that surround the rhabdoms. Light that has passed the rhabdom is reflected at the tapetum and thus receives a second chance of being absorbed, so enhancing the light sensitivity. The tracheoles that create reflecting mirrors around the rhabdoms fulfill also another function, namely to obstruct leakage of obliquely entering light towards neighboring rhabdoms and thus to prevent loss of spatial resolution (Land and Nilsson, 2002).

Well-developed tapeta, very similar to those of the nocturnal moths, exist in the superposition eyes of the diurnal moths and skippers. The tracheoles isolate the rhabdoms from each other also in these cases, which is a quite sensible optical function, because obliquely traveling light could severely downgrade spatial acuity. Much less obvious is the action of the tapetal reflector created by tracheoles proximally of each rhabdom in the apposition eyes of most diurnal butterflies. Calculations show that the sensitivity enhancement by the tapetum



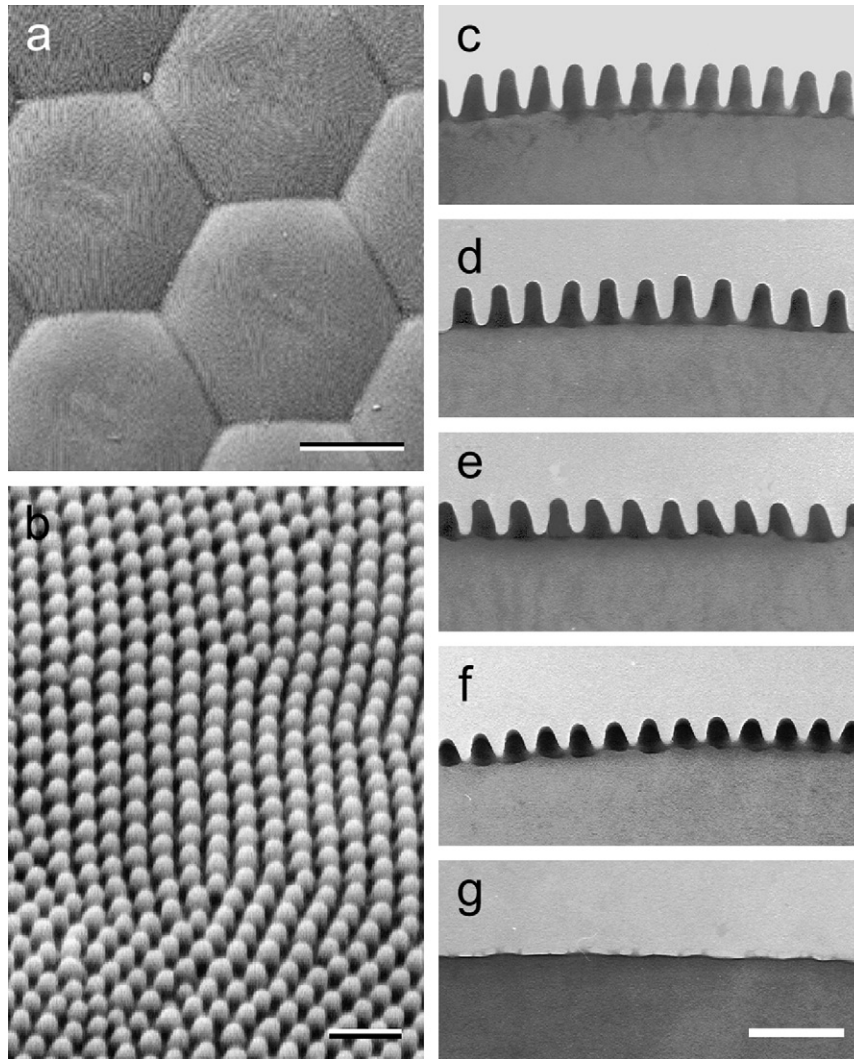


Fig. 6. Corneal nipple arrays of butterflies. (a, b) Scanning electron microscopy of facets of the cabbage white *Pieris napi*. (c–g) Transmission electron microscopy of the facet surface of the nymphalids *Bicyclus anynana* (c) and *Polygonia caureum* (d), the pierid *Pieris rapae* (e), the lycaenid *Pseudozizeeria maha* (f), and the papilionid *Papilio xuthus* (g). Bars, a: 10  $\mu$ m, b–g: 500 nm.

of apposition eyes can be only very minor, suggesting that the tapetum is a trait preserved during the transition from superposition to apposition eye. Considering its low yield, it might vanish without great functional loss, however. In fact, whereas the Nymphalidae, Lycaenidae, and Pieridae possess tapeta, so that eye shine is visible with an epi-illumination microscope, the Papilionidae lack a tracheolar tapetum below the rhabdom, and thus they do not exhibit eye shine (Miller, 1979). Apparently the papilionids lost the tapetum in the course of evolution. Actually, the orange tips (Anthocharidini, Pieridae) is another group of butterflies that lacks the tapetum (and the eye shine), suggesting that there may be more cases of butterflies where the tapetum has been shed (Stavenga et al., 2005).

#### 4. Wing coloration

The coloration of nocturnal moths is generally rather inconspicuous, and when there are clear color patterns they tend to

be disruptive, so that they serve to camouflage the moths from predators. Many crepuscular moths and especially the diurnal moths and butterflies are famous for their bright colors, however. The evolution of wing colors, for display and/or camouflage, will presumably have influenced the evolution of visual color discrimination, depending on the animal's behavior and its habitat.

The small white, *P. rapae*, offers an interesting example of the biology of wing coloration. Both sexes of this butterfly species are rather featureless for human eyes, except for slight differences in the black spots, small wing areas where the wing scales contain melanin. The white color is caused by strongly scattering structures in the wing scales (Stavenga et al., 2004). The reflectance is only high above 450 nm, but it is minor below 400 nm, because the scales of male *P. rapae crucivora* contain a substantial amount of UV-absorbing pteridins (Obara, 1970; Stavenga et al., 2004); see (Fig. 7).

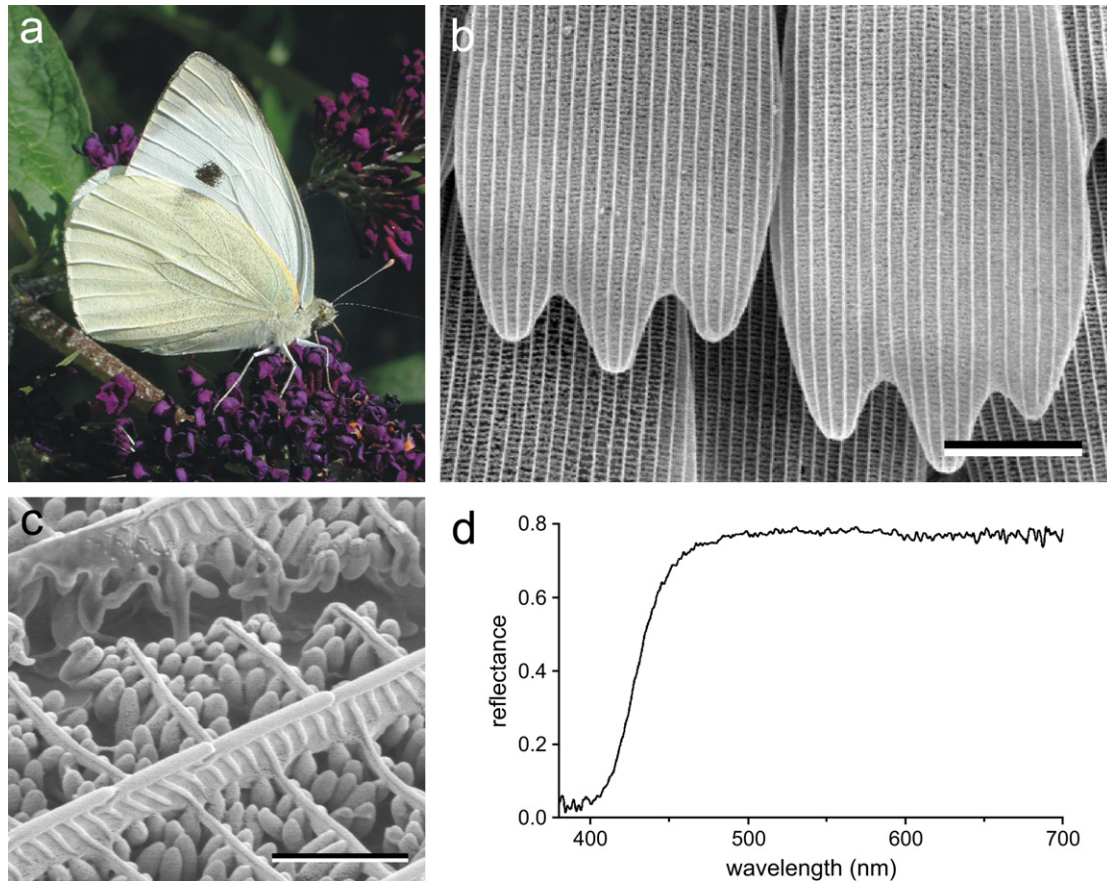


Fig. 7. Coloration of pierid butterflies. (a) The large white, *Pieris brassicae*. (b) The wing scales are marked by longitudinal ridges and cross-ribs. (c) The cross-ribs are studded with ovoid beads. Part of the structure has been artificially removed to show the highly involutioned wing scale structure. (d) The wing scales strongly scatter, but due to pteridin pigment, which strongly absorbs in the UV, the reflectance is low in the UV.

This creates a distinct coloration for the butterflies, because of their capacity to detect UV light. The wings of female *P. rapae crucivora* hardly contain absorbing pigment, so that they are whitish, even for butterfly vision. As was described above, the eyes of male and female *P. rapae crucivora* differ in the short-wavelength receptors (Table 1). The difference is caused by a violet-absorbing pigment in the eyes of the males, which can be observed in vivo via its fluorescence. Presumably the short-wavelength receptors are involved in color discrimination in the blue and (ultra)violet wavelength ranges, as the males search for females specifically in the shade where UV contrast is strongest (Obara, 1970).

The European subspecies *P. rapae rapae* does not feature the distinct sexual dichroism of the Japanese small white (Obara and Majerus, 2000). The sexual dichroism of the small white appears to change gradually along the globe (Obara, personal communication), but the evolutionary forces that have driven this global gradient need further study.

Sexual dichroism is a common feature of the sulphurs (Coliadinae), the subfamily that together with the whites (Pierinae) constitutes the Pieridae. The sulphurs have a dominant yellow or orange coloration, because ultraviolet- and blue-absorbing pteridins suppress the scattering in the short-wavelength range. The wings of the males of most sulphur species are not black

in the ultraviolet, however, because the scales at the upper (dorsal) side are highly folded, thus forming multilayers that strongly reflect in the ultraviolet (Ghiradella et al., 1972; Silberglied and Taylor, 1973; Kemp et al., 2005). The UV iridescence combined with the yellow/orange scattering creates a purplish color, at least as seen by the butterflies. A purple color is indeed also observed by humans in the tips of the male *Colotis regina*, where a blue iridescence is combined with red scattering. The latter results from the presence of a pigment that absorbs at all wavelengths except in the red.

The coloration methods and sexual dichroism of the Pierinae and Coliadinae are quite opposite. The wing reflectance of the whites, at least the males, is generally low in the UV and high at wavelengths above 450 nm. The wing reflectance of the male sulphurs is high in the UV, low in the blue and high in the yellow (above 550 nm). A mixture of both strategies appears to be employed by males of many *Colotis* species (Fig. 8). The tips of the dorsal wings are like that of Coliadinae, that is, a short-wavelength iridescence is combined with scattering at longer wavelengths. The remaining parts of the dorsal wings are rather like the wings of the whites, that is a low reflectance in the UV is combined with a high scattering above 450 nm (Stavenga et al., 2006). Because the Coliadinae are ancestral to the Pierinae (Braby, 2005; Braby et al., 2006),

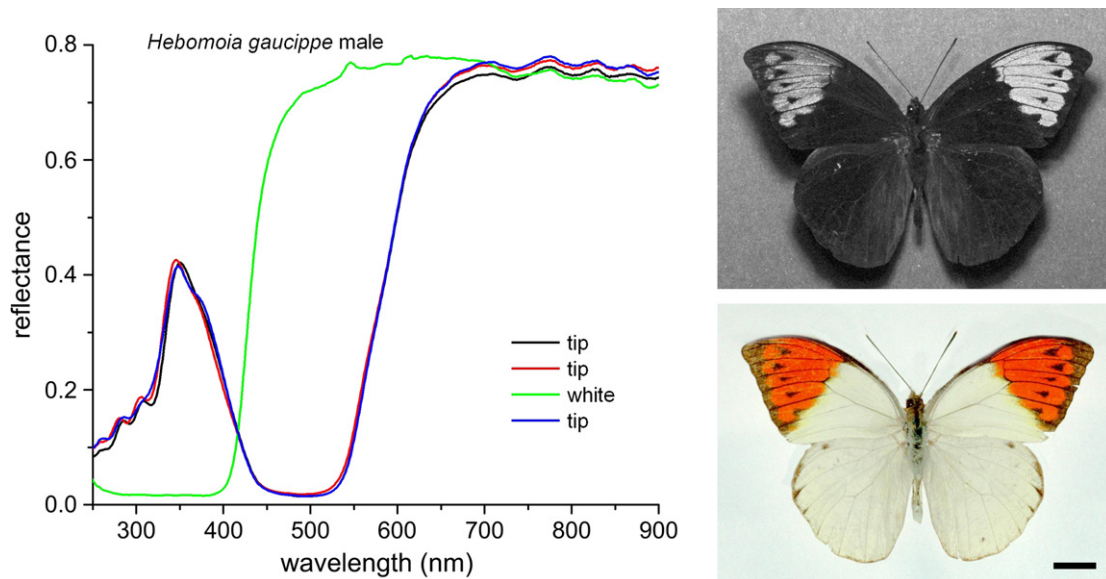


Fig. 8. Reflectance spectra of the male pierid *Hebomoia glaucippe*. Male butterflies of the *Colotis* group have red or orange wing tips that are UV or violet iridescent. The main part of the wings have white scattering scales with UV-absorbing pigment (compare Fig. 7d).

it may be speculated that the *Colotis* group forms an intermediate stage in the evolution of the sulphurs and the whites.

The spectral properties of the photoreceptors have presumably co-evolved with the wing coloration (see e.g. Bernard and Remington, 1991; Sison-Mangus et al., 2006). At least, the present evidence, although scanty, gained for a number of insect species favors the view that the spectral sensitivity of the photoreceptors is tuned to the body coloration of the conspecifics. Nevertheless, even if future research will reveal only minor differences between the retinal photoreceptors of the whites and sulphurs, it may be expected that the neural systems of the optical ganglia that process spectral information have evolved in such a way that the discrimination of conspecifics by their colors is optimized.

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